THE EFFACED STYGINID TRILOBITE *THOMASTUS* FROM THE SILURIAN OF VICTORIA, AUSTRALIA

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ABSTRACT. *Thomastus* is a blind effaced styginid trilobite that occurs in strata of Wenlock age in Victoria, Australia. The genus is most closely related to *Bumastella* and *Illaenoides*, with which it shares characters such as a highly convex cephalon, the absence of the omphalus and the anterolateral internal pit, a weakly forwardly converging facial suture, a transverse furrow in front of the articulating flange on the posterior fixigenal margin, and a pygidium with a deep holcos. Of the four species previously assigned to *Thomastus*, *T. collusor* and *T. vicarius* are considered to be synonyms of the type species *T. thomastus*. One new species, *T. aops*, is described.

THE trilobite *Thomastus* Öpik, 1953 is known only from strata of Wenlock age cropping out in the region between Melbourne and Heathcote in central Victoria, Australia (Text-fig. 1). Four species have been assigned to the genus: *T. thomastus* Öpik, 1953, *T. collusor* Öpik, 1953, and *T. vicarius* Öpik, 1953, all from the Wapentake Formation in the Heathcote district; and *T. jutsoni* (Chapman, 1912) from the Anderson Creek Formation at Bulleen and Balwyn in the eastern suburbs of Melbourne. Another species, *T. aops* sp. nov., from the Bylands Siltstone in the Bylands area, is newly described herein.

Since *Thomastus* was established it has remained poorly understood because of the indifferent preservation of many of the specimens, and because of the limited material on which three of the four previously named species are based. The opportunity to revise the genus has been provided by an enlarged collection of material acquired through recent field collecting and the transfer to the Museum of Victoria of specimens formerly housed in the Geological Survey of Victoria and the University of Melbourne.

FAUNAS AND AGE

Heathcote. The Wapentake Formation in the Heathcote district consists of approximately 1900 m of siltstones and sandstones conformably overlying the Costerfield Siltstone (Text-fig. 2). Low in the Wapentake Formation is a relatively thin band of siltstone characterized by the presence of siliceous concretions, many of them containing fossils, of which *Thomastus thomastus* is the most abundant. This horizon was named the '*Illaenus*' band by Chapman and Thomas (1935) and Thomas (1937), who considered it to mark the base of the Wapentake Formation. However, Rickards and Sandford (in press) note that the fauna of the '*Illaenus*' band ranges well above and below this level, and they redefined the base of the Wapentake Formation 400 m lower in the sequence at the appearance of prominent sandstones. Conformably overlying the Wapentake Formation are 2200 m of sandstones, siltstones and mudstones, named the Dargile Formation by Thomas (1937); Rickards and Sandford (in press) assign these beds to the Yan Yean Formation (lower) and the Melbourne Formation (upper), and raised the Dargile Formation to group status to incorporate the entire Wenlock–lowermost Ludlow sequence.

The fauna of the '*Illaenus*' band, described by Öpik (1953) and revised by Talent (1964), includes brachiopods, bryozoans, bivalves, gastropods, trilobites, ostracodes and conulariids. Some of the

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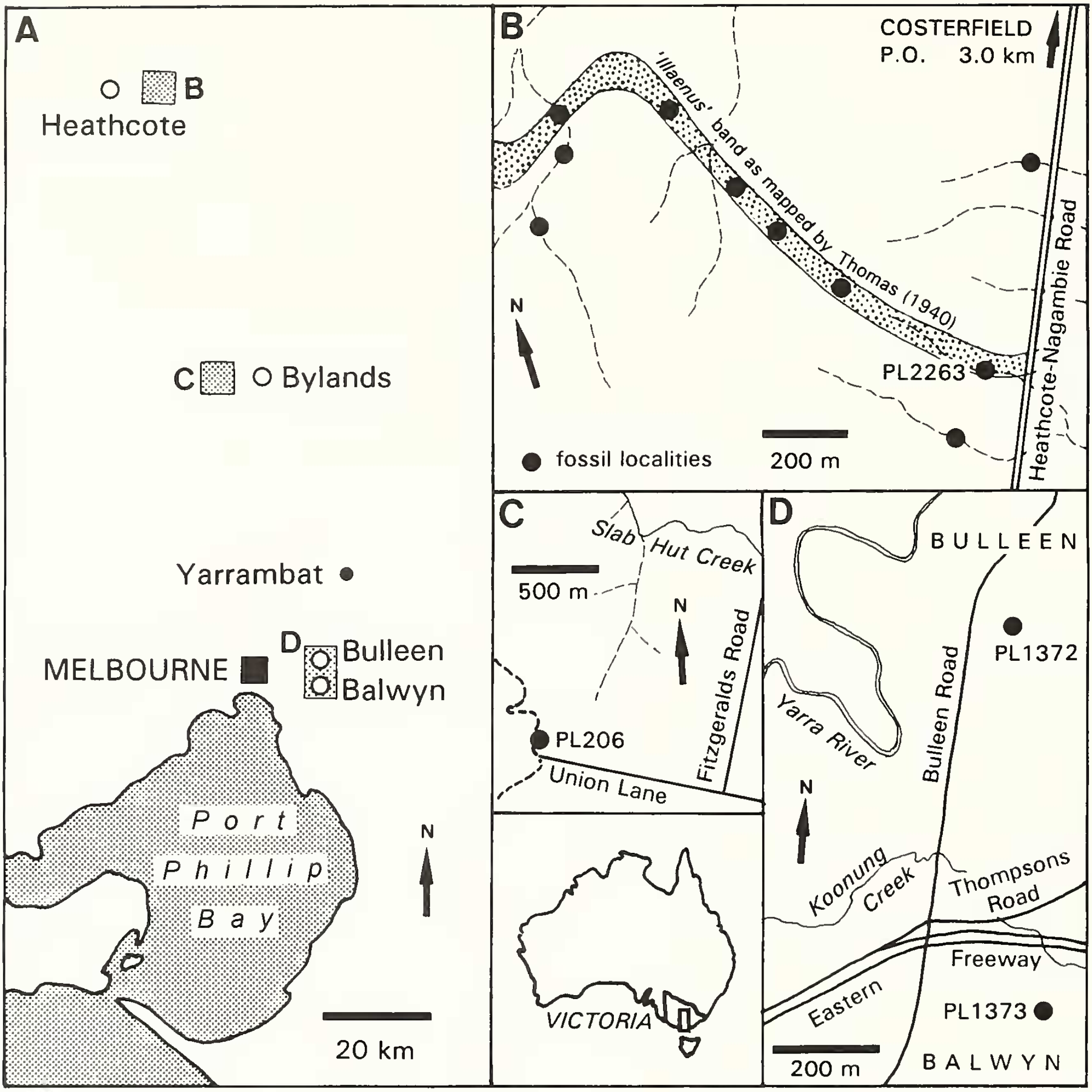
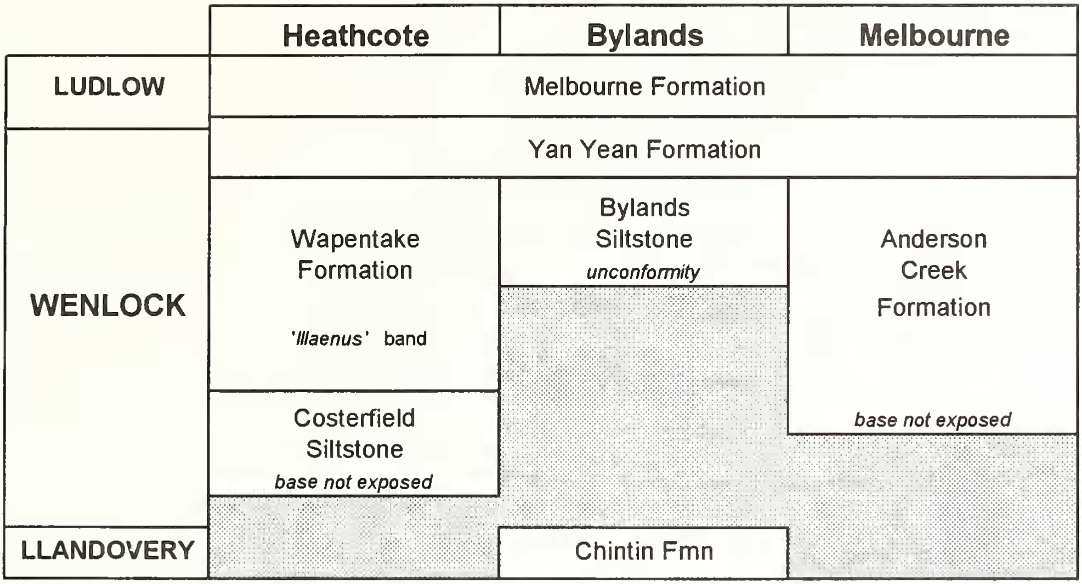


TEXT-FIG. 1. A, map of central Victoria showing localities from which *Thomastus* has been recorded; approximate areas of figures B–D indicated by shaded squares. B–D, location of *Thomastus* localities in the Heathcote, Bylands and Bulleen-Balwyn areas. Inset shows location of Victoria and area of figure A in Australia.

siliceous nodules from the band were interpreted by Öpik as coprolites, but they are probably concretions. At least 80 per cent. of the trilobites recovered from the band belong to *Thomastus*, but Öpik (1953) also described '*Phacops*' *typhlagogus* (= *Ananaspis*; see Campbell 1967, p. 32), *Dalmanites athamas* and '*Dalmanitina* (*Eudolatites*)' *aborigenum* (a junior synonym of *Dalmanites athamas*; see below). Other trilobites that we have identified from limited material are *Maurotarion* sp., *Trimerus*? sp., and indeterminate specimens of a calymenid, a proetid and an odontopleurid; the last includes a cephalon and the isolated thoracic segment identified by Öpik (1953) as *Ceratocephala* sp.



TEXT-FIG. 2. Upper Llandovery–Lower Ludlow stratigraphy at localities where *Thomastus* has been collected; stratigraphical terminology follows Rickards and Sandford (in press).

The '*Illaenus*' band was considered by Öpik (1953, p. 10) to be of mid to late Llandovery age, based mainly on the presence of graptolites identified as *Climacograptus hughesi* and *Monograptus* cf. *jaculum*. The present whereabouts of these graptolite specimens are unknown, so their identifications cannot be verified. However, the occurrence of *Ananaspis typhlagogus*, belonging to a genus not known to range below the Wenlock, and the presence of earliest Ludlow (*nilssoni* Biozone) graptolites at a stratigraphical level 2800 m higher in the sequence (high in the overlying Yan Yean Formation; see Rickards and Sandford in press, fig. 4), indicate that the Wapentake Formation, including the '*Illaenus*' band, is of Wenlock age.

Bylands. Siltstones at a locality in the Bylands area contain a sparse but diverse fossil fauna, including trilobites, articulate and inarticulate brachiopods, bivalves, gastropods, nautiloids, hyolithids, conulariids and carpoids. Apart from the new species of *Thomastus*, *T. aops*, trilobites present include *Decoroproetus*?, a species of *Ananaspis* distinct from *A. typhlagogus*, a pygidium of *Struveria*?, a new genus of blind acastid, a thoracic segment of an indeterminate homalonotid, *Dicranurus*, and other indeterminate odontopleurids. Mapping by VandenBerg (1992) placed this locality at the top of the Chintin Formation; Rickards and Sandford (in press), however, included the locality in their newly named Bylands Siltstone, which they considered to overlie the Chintin Formation disconformably (Text-fig. 2). The presence of *Ananaspis* indicates that the strata at this locality are no older than Wenlock, and this age is consistent with the occurrence of graptolites of the latest Wenlock *ludensis* Biozone low in the overlying Yan Yean Formation at a locality about 7 km to the east (PL1675 = locality Q2 of Williams 1964, fig. 2; see Rickards and Sandford in press, fig. 4).

Blind trilobites are rare in the Silurian, so it is noteworthy that two blind forms, *Thomastus* and a new acastid genus, are the most common trilobites in the Bylands fauna. *Thomastus* also dominates the fauna in the '*Illaenus*' band at Heathcote. With the possible exception of the homalonotids, which generally have relatively small eyes, none of the other trilobites present at either locality appears to have reduced eyes. The two species of *Ananaspis* have eyes of normal size for the genus, and the size of the palpebral lobes in *Decoroproetus*? and *Dicranurus* from Bylands, and *Maurotarion* from Heathcote, indicate that the eyes in these forms were also of normal size. In the other trilobites occurring at Bylands and Heathcote neither the eyes nor the palpebral lobes are preserved, so their size is unknown.

A fauna of blind or almost blind trilobites from the Arenig of South Wales was described by Fortey and Owens (1987), who named it the atheloptic association. It was found together with large-eyed trilobites of the cyclopygid families, but these were considered to have been mesopelagic forms inhabiting the water column above the benthic fauna of blind or almost blind forms. The trilobites at Bylands and Heathcote lacking reduced eyes do not have the morphology of pelagic forms (e.g. a wide axis) and would have been benthic like *Thomastus* and the blind acastid. Hence, the blind trilobites at Bylands and Heathcote, unlike those in the atheloptic assemblage of Fortey and Owens, occurred together with normal-eyed forms in a natural benthic community.

Melbourne. The Anderson Creek Formation in the Melbourne district was considered by VandenBerg (1988, p. 107) to consist of 2300 m of sandstones, siltstones and minor conglomerates of late Llandovery to early Ludlow age. Rickards and Sandford (in press), however, restricted the unit to strata of early and mid Wenlock age, with a thickness of about 1300 m; overlying strata of latest Wenlock to early Ludlow age were assigned by Rickards and Sandford to the Yan Yean and Melbourne formations.

The Anderson Creek Formation is mostly unfossiliferous, but sparse shelly faunas and graptolites, mostly undescribed, are known from a few scattered localities. *Thomastus jutsoni*, known only from two specimens from separate localities near the top of the formation (as redefined by Rickards and Sandford), is the only trilobite described. Graptolites from the formation listed by Rickards and Sandford (in press, fig. 4) are indicative of the *riccartonensis* and *testis* biozones.

SYSTEMATIC PALAEONTOLOGY

Repositories and terminology. Specimens are housed in the invertebrate palaeontological collections of the Museum of Victoria (NMV), and the Commonwealth Palaeontological Collection, Australian Geological Survey Organisation, Canberra (CPC). For specimens previously housed in the Geological Survey of Victoria (GSV) and the Geology Department of the University of Melbourne (MUGD), the old registration numbers of those institutions are given as well as the new Museum of Victoria numbers. Locality numbers with a PL prefix are listed in the invertebrate fossil locality register of the Museum of Victoria.

Morphological terminology follows Holloway and Lane (1998, p. 863).

Note on 'Dalmanitina (Eudolatites)' aborigenum. This species was based by Öpik (1953, p. 26, pl. 10, figs 85–87) only on an incomplete fixigena and a fragmentary pygidium from the '*Illaenus*' band of the Wapentake Formation in the Heathcote district. The fixigena, the holotype of the species, actually belongs to the Dalmanitinae rather than to the Dalmanitininae or to the Mucronaspidinae (see Holloway 1981), as shown by the lanceolate posterior border furrow that does not meet the lateral border furrow distally, and by the broad, flattened genal spine. Öpik believed that the course of the posterior branch of the facial suture suggested that the eye, which is not preserved, was very small and set far forward, unlike the large eyes of most Dalmanitinae. However, only the abaxial part of the suture is preserved, and its course is similar to that in other large-eyed Dalmanitinae, in which the suture is deflected anterolaterally from the back of the eye in a convex forwards curve (e.g. Campbell 1967, pl. 18, fig. 2). We therefore assign this specimen to *Dalmanites athamas* and consider *aborigenum* to be a junior synonym of that species. The paratype pygidium of *aborigenum* does not belong to *D. athamas*, as the pleural furrows are short (exsag.) and sharply incised instead of being expanded (exsag.) and asymmetrical in profile. We consider the specimen to be too incomplete for reliable generic assignment.

Suborder ILLAENINA Jaanusson, 1959
Family STYGINIDAE Vogdes, 1890
Genus THOMASTUS Öpik, 1953

Type species. Thomastus thomastus Öpik, 1953 from the Wapentake Formation (Wenlock) of central Victoria, Australia; original designation.

Diagnosis. Cephalon highly convex (sag., tr.), curving through more than 90° in sagittal line, very steep anteriorly. Glabella narrowest at or behind lunette; axial furrow very weak or absent in front of lunette. Omphalus and anterolateral internal pit absent. Posterior part of fixigena with distinct transverse furrow in front of articulating flange. Eyes absent; facial suture gently convex abaxially, exsagittally aligned or weakly diverging forwards in posterior part, converging forwards in anterior part, situated far from axial furrow. Librigena narrow (tr.), posterior margin concave in outline, genal angle with spine or more or less orthogonal. Cephalic doublure with vincular furrow running oblique to posterior margin; rostral plate lenticular in outline, lacking posterior flange; connective suture meeting hypostomal suture rather far from sagittal line. Hypostome with middle furrow and maculae very weak or absent; lateral and posterior borders narrow, lacking shoulder. Thorax with ten segments; axis 50–60 per cent. segmental width; axial furrow distinct; pleurae adaxial to fulcrum as wide (tr.) as or wider than abaxial to fulcrum. Pygidium much less convex than cephalon; anterior margin with distinct transverse portion just adaxial to articulating facet; holcos well developed.

Remarks. In erecting *Thomastus*, Öpik (1953, pp. 22–23) proposed an ancestry for it in *Bumastus*, and suggested that it might perhaps be included in *Bumastus* as a subgenus, although he preferred to regard it as an independent genus in order to preserve the concept of *Bumastus* as having characteristically large eyes. A relationship with *Bumastus* was accepted by Jaanusson (1957, p. 93; 1959, p. 374) who assigned *Thomastus* to the Bumastinae (*sensu* Raymond 1916). Lane and Thomas (1983, pp. 156–157), however, included *Thomastus* in a list of genera they assigned to the Illaenidae, whereas they placed *Bumastus* in the Styginidae. We do not consider that *Thomastus* belongs to the Illaenidae, because of the absence of an upwardly and forwardly curved posterior flange on the rostral plate. We agree with Öpik and Jaanusson that the affinities of *Thomastus* lie with *Bumastus*, although we interpret the latter in a more restricted sense (see Holloway and Lane 1998, p. 872) and do not consider it to be most closely related to *Thomastus*. In our opinion, *Thomastus* is most closely related to *Bumastella* Kobayashi and Hamada, 1974 (see Holloway and Lane 1998) and *Illaenoides* Weller, 1907. Characters shared with those genera include the extreme convexity of the cephalon, the absence of the omphalus and anterolateral internal pit, the facial suture that converges weakly forwards, the transverse furrow on the posterior part of the fixigena in front of the articulating flange, and the deep pygidial holcos. Apart from the presence of eyes, *Illaenoides* differs from *Thomastus* in that the cephalic axial furrow converges forwards more weakly behind the lunette, the facial suture is situated closer to the axial furrow, the genal angle is more rounded, and the hypostome is more elongated with a distinct posterior lobe of the middle body. *Bumastella* differs from *Thomastus* in having eyes, the posterior cephalic margin is deflected strongly backwards abaxial to the fulcrum, the lunette is situated farther forwards in dorsal view, the facial suture is situated closer to the axial furrow, the genal angle is broadly rounded, the rostral plate is subtriangular in outline rather than lenticular, the thoracic axis narrows more strongly backwards, so that the pleurae on the posterior thoracic segments are wider adaxial to the fulcrum, and the pygidium is more transverse.

In thoracic and pygidial morphology, including the well developed holcos, *Thomastus* shows similarities with *Opsypharus* Howells (1982, p. 10, pl. 2, figs 8–20), but striking differences in the cephalon indicate that the two genera are not closely related. The differences in *Opsypharus* include the low convexity of the cephalon, the presence of the omphalus, the axial furrow extending in front of the lunette, the much narrower fixigena, the strongly divergent anterior and posterior branches of the facial suture, the wide librigenae with shallow lateral border furrow, and the well rounded genal angle.

Thomastus thomastus Öpik, 1953

Plate 1, figures 1–16

1937 *Illaenus* sp.; Thomas, p. 66.
1953 *Thomastus thomastus* Öpik, p. 23, pl. 8, figs 61–71; text-fig. 8.
1953 *Thomastus collusor* Öpik, p. 24, pl. 9, figs 72–74.
1953 *Thomastus vicarius* Öpik, p. 24, pl. 9, figs 75–79.
1957 *Thomastus vicarius* Öpik; Jaanusson, p. 94.
1964 *Thomastus thomastus* Öpik; Talent, p. 47.
1964 *Thomastus collusor* Öpik; Talent, p. 47.
1964 *Thomastus vicarius* Öpik; Talent, p. 48.
non 1975 *Thomastus thomastus* Öpik; Fletcher, p. 69, fig. 2B–D.

Holotype. Dorsal exoskeleton NMV P52474 (*ex* GSV 36570), figured Öpik (1953, pl. 8, figs 61–62, text-fig. 8), Plate 1, figures 1, 4, 15; from locality PL2263 (= F44 of Thomas 1940; and locality 44, Parish of Heathcote in Talent 1964, fig. 1), Heathcote district, Victoria (grid reference CV03021272 on the Costerfield 1:25000 topographic sheet 7824-2-3).

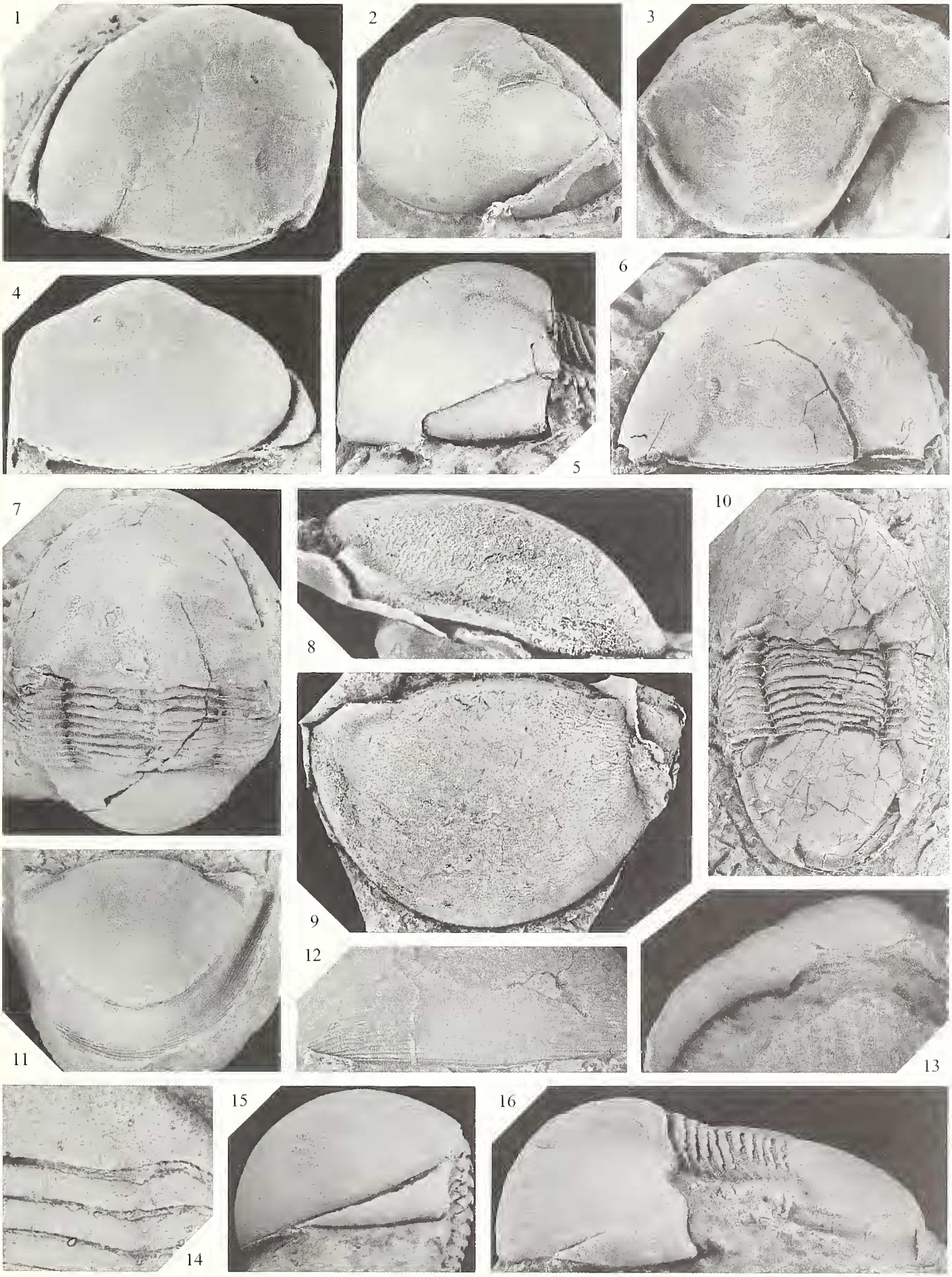
Paratypes. From the same locality as the holotype: dorsal exoskeleton NMV P52475 (*ex* GSV 36573, figured Öpik 1953, pl. 8, figs 63–64). From locality PL2269 (= F51 of Thomas 1940; and locality 51, Parish of Heathcote in Talent 1964, fig. 1), Heathcote district, Victoria (grid reference CV06401145): dorsal exoskeleton NMV P52476 (*ex* GSV 46602; Öpik 1953, pl. 8, figs 65–66); incomplete dorsal exoskeleton NMV P52478 (*ex* GSV 46604, 46619, counterparts; Öpik 1953, pl. 8, figs 69–70); incomplete cranidium NMV P52479 (*ex* GSV 46620; Öpik 1953, pl. 8, fig. 71); hypostome NMV P52477 (*ex* GSV 46599; Öpik 1953, pl. 8, fig. 67). From locality PL1460, Heathcote district, Victoria (grid reference CV02531335): incomplete cranidium and thorax NMV P139848 (*ex* GSV 46570; not illustrated). From 'South Heathcote': dorsal exoskeleton NMV P140676 (*ex* MUGD 1959; Öpik 1953, pl. 8, fig. 68).

Type material of T. collusor. Öpik (1953, p. 24) stated that he had identified three specimens of this species, but the only specimen that can be located now is the holotype, an incomplete cephalon and partial thorax NMV P52480 (*ex* GSV 46631; Öpik 1953, pl. 9, figs 72–74), from locality PL2269.

Type material of T. vicarius. Holotype: dorsal exoskeleton CPC 691, figured Öpik (1953, pl. 9, figs 75–76); the counterpart external mould, consisting of the thorax and pygidium but lacking the cephalon, is NMV P139889;

EXPLANATION OF PLATE 1

Figs 1–16. *Thomastus thomastus* Öpik, 1953; lower part of Wapentake Formation (Wenlock), Heathcote district, Victoria. 1, 4, 15, NMV P52474, holotype; locality PL2263; dorsal exoskeleton. 1, dorsal view of cephalon. 4, anterior view. 15, lateral view of cephalon and part of thorax. All ×2·25. 2, NMV P147066; locality PL2263; cranidium, oblique view; ×1·5. 3, NMV P139827; '*Illaenus*' band, exact locality uncertain; hypostome, ventral view; ×3. 5–6, NMV P139977; locality PL2263; dorsal exoskeleton. 5, lateral view of cephalon. 6, dorsal view of cephalon. Both ×2. 7, NMV P139887; locality PL386; dorsal exoskeleton, dorsal view; ×1·5. 8–9, NMV P139979; locality PL2263; latex cast of pygidium. 8, lateral view; ×2·75. 9, dorsal view; ×2. 10, NMV P139914; from '2 km west of Costerfield'; dorsal exoskeleton, dorsal view; ×1·25. 11, NMV P139906; locality PL2263; pygidium, dorsal view; ×1·5. 12, NMV P139864; locality PL2269; incomplete cranidium, detail of anterior part in anterior view showing terrace ridges; ×2·5. 13, NMV P139932; '*Illaenus*' band, exact locality uncertain; cephalon, ventral view showing rostral plate; ×2·5. 14, NMV P139839 (ex GSV 36575); locality PL2263; incomplete dorsal exoskeleton, detail of back of cranidium and front of thorax showing sculpture; ×3·75. 16, NMV P139922; '*Illaenus*' band, exact locality uncertain; dorsal exoskeleton, lateral view; ×1·75.



SANDFORD and HOLLOWAY, *Thomastus*

collection locality not recorded by Öpik (1953) but is probably PL2263. Paratypes: dorsal exoskeleton NMV P140675 (*ex* MUGD 1960; Öpik 1953, pl. 9, figs 78–79), from 'South Heathcote'; incomplete pygidium NMV P52481 (*ex* GSV 46624; Öpik 1953, pl. 9, fig. 77), from locality PL2269.

Other material. NMV P33135, P55955–P55956, P55959–P55965, P139806–P139847, P139849–P139864, P139975–P139888, P139890–P139984, P146118, P147047–P147048, P147058–P147061, P147066–P147069, from various localities in the Heathcote district.

Horizon. Wenlock Series; Wapentake Formation.

Diagnosis. Glabella narrowest at lunette. Facial suture gently and evenly curved in dorsal view, almost exsagittally aligned at posterior end, converging anteriorly. Librigena slightly wider than fixigena posteriorly; posterior margin of librigena weakly concave in outline; genal angle orthogonal or with very short spine. Pygidium moderately convex; lateral margin weakly arched upwards; holcos non-existent posteriorly; doublure angular in cross section anteriorly.

Description. Cephalon in dorsal view *c.* 160 per cent. as wide as long (sag.), widest posteriorly; anterior outline parabolic, posterior margin more-or-less transverse; in lateral view, cephalon almost as high as long, vertical or slightly overhanging anteriorly, highest point situated well in front of posterior margin and opposite lunette. Axial furrow describing abaxially concave arc, shallow behind lunette, faint to effaced in front of lunette. Small, conical apodeme present just in front of posterior cephalic margin, at junction of axial furrow and transverse furrow in front of articulating flange. Glabella forming low arch (tr.) at posterior margin, retaining slight independent convexity (tr.) as far forward as lunette; width of glabella almost 50 per cent. maximum cephalic width posteriorly, width at lunette *c.* 60 per cent. posterior width. Lunette weakly impressed, situated at *c.* 40 per cent. of cephalic length (sag.) in dorsal view. Fixigena wide, decreasing in convexity (tr.) anteriorly, width opposite lunette equal to width of glabella measured across same transverse line. Posterior fixigenal margin gently flexed downwards and backwards about half way between axial furrow and posterior end of facial suture. Librigena as wide posteriorly as fixigena, narrowing forwards, sloping very steeply abaxially; genal angle with short spine (Pl. 1, fig. 16) or almost orthogonal; posterior librigenal margin always gently concave adaxial to genal angle. Facial suture in lateral view horizontal or sloping backwards slightly at posterior end, thereafter sloping forwards at *c.* 20° to horizontal.

Cephalic doublure steeply inclined and gently convex posteriorly, increasing greatly in convexity anteriorly, its inner edge deeply embayed medially by strongly transversely arched hypostomal suture. Vincular furrow shallow, bounded in front by a ridge that is subangular in cross section at inner edge of doublure and dies out abaxially. Rostral plate *c.* 20 per cent. as wide posteriorly as anteriorly, gently convex (sag., exsag.) over most of its length, weakly concave (sag., exsag.) just in front of posterior margin; posterior margin gently concave in outline. Connective suture concave abaxially in anterior half and gently convex abaxially in posterior half, converging backwards at *c.* 60° to sagittal line overall.

Hypostome twice as wide across anterior wings as long (sag.), outline excluding anterior wings semielliptical. Middle body inflated, in transverse profile strongly rounded in sagittal line and flattened on flanks, in lateral profile weakly concave just in front of posterior border furrow; middle furrow and maculae indistinguishable. Lateral border rounded (tr.), narrowing backwards; lateral border furrow increasing in depth slightly towards anterior end. Posterior border very short (sag., exsag.), with sharply rounded crest; posterior border furrow long (sag., exsag.), shallow, poorly differentiated from middle body. Posterior wing triangular, situated opposite posteromedial edge of middle body.

Thorax with axis gently arched (tr.), weakly expanding backwards in anterior half, narrowing more distinctly backwards in posterior half. Axial rings gently convex (sag., exsag.), expanding only very weakly medially; articulating furrow not defined. Portion of pleurae adaxial to fulcrum horizontal, successively increasing in width (tr.) from front to back of thorax. Abaxial to fulcrum, anterior segments strongly flexed backwards, posterior segments successively more weakly flexed backwards and curving forwards slightly distally. Close to posterior edge of segment on internal surface is a small, conical apodeme situated directly beneath axial furrow.

Pygidium 62 per cent. to more than 90 per cent. as long as wide, widest across posterior edge of articulating facet; posterior and lateral margins with strongest curvature medially. In lateral profile, pygidium highest at about half sagittal length. Articulating facet short (exsag.), extending adaxially about half anterior width (tr.) of pleura. Anterior width of axis (marked by forward arching of anterior margin between anterior ends of holcos) about half maximum width of pygidium. Holcos broad, well-rounded, deepest anteriorly where it runs subparallel to posterior edge of articulating facet, dying out opposite about 60 per cent. of pygidial length (sag.)

from anterior. Doublure widest medially where it is almost 30 per cent. sagittal length of pygidium. Anterolaterally, doublure divided into a flattened, gently abaxially sloping outer portion and a flattened, steeply inclined inner portion by a subangular flexure; posteromedially, this flexure fades, outer portion of doublure becomes gently convex and slopes weakly outwards, and inner portion becomes weakly concave and slightly less steeply inclined.

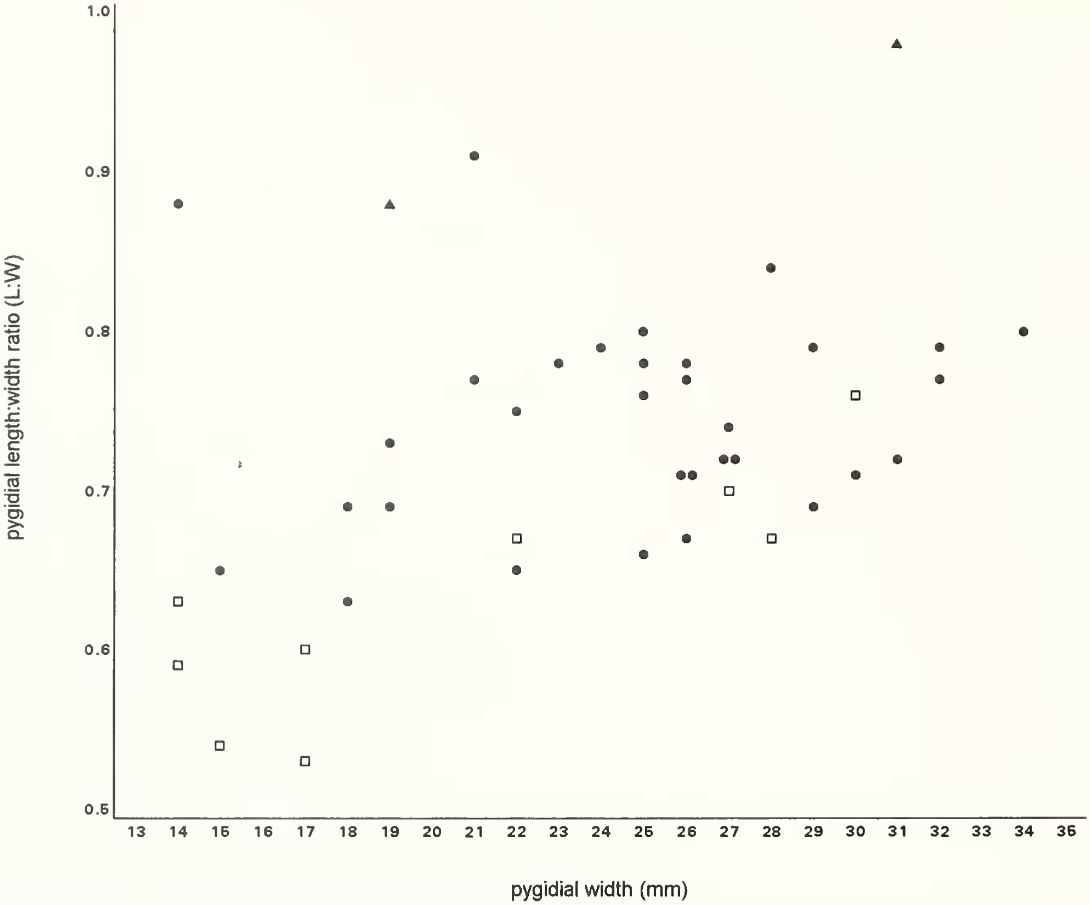
Sculpture. Cephalon with terrace ridges close to and running subparallel with anterior and posterior margins; away from margins, terrace ridges grade into coarse pits covering reminder of dorsal surface of cephalon. Thorax with terrace ridges running subparallel to anterior and posterior margins of segments. Terrace ridges on pygidium more extensive than on cephalon, running parallel with pygidial margins peripherally, becoming more transverse adaxially opposite pygidial midlength, grading into pits medially. Cephalic and pygidial doublures with terrace ridges running subparallel to margins; terrace ridges more closely spaced on outer part of cephalic doublure than on inner part, and very closely spaced on subangular flexure subdividing anterolateral part of pygidial doublure. Terrace ridges on hypostome run concentrically on lateral and posterior borders, and in convex-backwards arcs on middle body.

Remarks. Specimens of *T. thomastus* not preserved in concretions are flattened and crushed, as noted by Öpik (1953, p. 23), and the exoskeleton is commonly fractured into angular fragments (e.g. Pl. 1, fig. 10). Specimens in concretions are less deformed, but the steeply inclined librigenae are commonly displaced slightly inwards and upwards beneath the cranidium, resulting in the abaxial part of the fixigena lying above the librigena being broken off (e.g. Pl. 1, fig. 5). In all specimens, the surface of the exoskeleton is coated with a very thin layer of a grey or brown crystalline mineral that X-ray diffraction analysis has shown to be siliceous. Whether this mineral has partly replaced the outermost layers of the exoskeleton or has been deposited in a thin layer on internal and external moulds is unclear. However, in specimens in concretions, which are preserved in positive relief and have some of the characteristics of internal moulds (e.g. expression of apodemes), the siliceous coating commonly also shows details of external sculpture (e.g. Pl. 1, fig. 12). No muscle scars have been observed either on specimens preserved in positive relief or on the corresponding external moulds.

Two specimens, NMV P139900 and NMV P147066 (Pl. 1, fig. 2), each have a large swelling on the cheek situated fairly close to the axial furrow. In the first specimen the swelling is level with the back of the lunette in dorsal view, and in the second it is level with the front of the lunette. In neither is it possible, because of preservational factors, to determine whether there was a corresponding swelling on the opposite cheek. The swellings contain no evidence of lenses and therefore do not appear to be eyes. It is possible that they are non-functional remnants of eyes; if so, their position well adaxial to the facial suture indicates that the suture must have migrated from its former course. However, the slightly different position of the swellings in relation to the lunette in the two specimens leads us to believe that the swellings are not associated with eyes, and that they are probably pathological.

Many specimens of *T. thomastus*, especially those in concretions, are preserved in a posture in which, if the lateral margins of the cephalon are oriented in a horizontal plane, the thorax and pygidium slope steeply downwards and backwards. This posture, known as the bumastoid stance, is similar to the inferred life orientation of other highly convex illaenimorph trilobites (Bergström 1973, figs 13–14; Stitt 1976, text-fig. 6; Westrop 1983, fig. 3; Fortey 1986, fig. 7) and, as in those forms, suggests that *Thomastus* may have led a sedentary, infaunal, suspension feeding existence. Specimens of *T. thomastus* not in concretions are less commonly preserved in the life orientation; the greater compaction suffered by these specimens has in most cases caused the front of the cephalon to be rotated upwards so that the posterior edge of the occipital region has ridden over the first few axial rings of the thorax (Pl. 1, fig. 10).

It is normally considered that in trilobites adopting the bumastoid stance the pygidium and most of the thorax were buried in the sediment, and the cephalon protruded above the surface. Being blind, *Thomastus* may have lived with the top of its cephalon below the sediment surface, and used its anterior appendages to draw water into its burrow for feeding and respiration.



TEXT-FIG. 3. Plot of pygidial length:width ratio versus pygidial width for *Thomastus thomastus* (dots), *T. aops* (open squares) and *T. jutsoni* (triangles).

Variation in *Thomastus thomastus* in the shape of the genal angle is related to specimen size. The smallest cephalon (maximum width *c*. 13 mm) in which the shape of the genal angle is clear has a short genal spine subtending an angle of about 50°; with increasing specimen size, the genal spine decreases in length, and in the largest cephalon (maximum width *c*. 27 mm) with the genal angle preserved it is obtuse (*c*. 110°) and lacks a spine. Proportions of the pygidium vary considerably between specimens of similar size, but a general increase in elongation (L:W ratio) with increasing size can be recognized in the sample population (Text-fig. 3). Two specimens have pygidia as elongated as that of *T. jutsoni*, with L:W ratios close to 0·9, but these specimens resemble others of *T. thomastus* in having the narrowest part of the glabella situated at the lunette, instead of well behind the lunette as in *T. jutsoni* (see Table 1). Pygidia of *T. thomastus* have the lateral margin and the outer part of the doublure just behind the articulating facet weakly deflected upwards in a long (exsag.) arch (see Pl. 1, figs 8, 16), resulting in the doublure becoming angular in cross section (Pl. 1, fig. 11). This arch appears to match the ventral curvature of the librigenal margin, and presumably ensured a close fit between the cephalon and pygidium on enrolment.

Doubts about the distinctness of *T. collusor* and *T. vicarius* were raised by Talent (1964, p. 48), who suspected that one of them may be a sexual dimorph of *T. thomastus*. We consider both *collusor* and *vicarius* to be synonyms of *T. thomastus*. Öpik (1953, p. 25) considered *T. vicarius* to be distinguished from *T. thomastus* mainly by the more widely spaced terrace ridges on the doublure, especially the pygidial doublure. Our observations indicate that the spacing of the terrace ridges is greater in larger specimens than in smaller ones, and we attribute the relatively wide spacing in the types of *vicarius* to the large size of these specimens. Other features in which Öpik considered *vicarius* to differ from *T. thomastus* were a less inflated cephalon with a sub-triangular rather than 'broad elliptical' outline, rounded rather than spinose genal angles, and a wider thoracic axis at the fourth segment. We can detect no significant differences in the convexity and outline of the cephalon nor in the relative width of the axis, and the genal angle is incomplete in both the holotype and one of the paratypes of *vicarius* but does not appear to have been rounded. Öpik (1953, p. 24) distinguished *T. collusor* from *T. thomastus* by the rounded genal angle, the more inflated fixigenae, the deeper transverse furrow ('pleuro-occipital furrow') on the posterior part of the fixigena, the transverse curvature of the glabella just in front of the posterior margin, the coarser pitting of the exoskeleton, and the subparallel course of the thoracic axial furrow. In the holotype of *collusor* (Öpik 1953, pl. 9, figs 72–74), the only member of the type series that can now be recognized, the genal angle is broken so its shape is indeterminate, and we can detect no significant differences from *T. thomastus* in the other characters mentioned.

The horizon from which Fletcher (1975) recorded 'numerous cephala and pygidia' of *Thomastus thomastus* in the Cobar district of western New South Wales is uncertain. Fletcher gave the horizon as the Mallee Tank Beds, but that stratigraphical name is obsolete. The specimens may have come from either the Baledmund Formation or the Burthong Formation, both considered to be of Lochkovian age (MacRae 1987); however, we do not know of any other records of effaced styginids in rocks younger than Silurian. Fletcher stated that *T. thomastus* is also very common in the Rosyth Limestone (Upper Llandovery; Pickett 1982, fig. 18) near Orange, *c.* 400 km south-west of Cobar. The specimens illustrated by Fletcher (1975, fig. 2B–D) are internal moulds of three pygidia, two from the Cobar district and one from the Rosyth Limestone. They differ from pygidia of *T. thomastus* in lacking the distinct transverse portion of the anterior margin adaxial to the articulating facet, the entire anterior margin instead forming an almost continuous curve with the facet. In addition, there is no holcos in the specimen from the Rosyth Limestone, and probably in the specimens from Cobar; in the latter specimens the lateral part of the dorsal surface is broken away, revealing the external mould of the doublure, but there is no trace of a holcos anteromedially. These differences preclude assignment of the specimens to *Thomastus*.

Thomastus aops sp. nov.

Plate 2, figures 1–10

1988 *Thomastus* cf. *thomastus* Öpik; VandenBerg, p. 105.
1992 *Thomastus* cf. *thomastus* Öpik; VandenBerg, p. 44.

Derivation of name. Greek 'blind', referring to the absence of eyes.

Holotype. Dorsal exoskeleton NMV P139969, figured Plate 2, figure 8; from locality PL206, near the western end of Union Lane, Bylands, Victoria (grid reference CU154644 on the Kilmore 1:25,000 topographic sheet 7823-2-1).

Paratypes. Dorsal exoskeletons NMV P139339, P139345–P139346, P139968, P139970–P139973; pygidia with incomplete thoraces NMV P139340, P139343; pygidium NMV P139966; all from the same locality as the holotype.

Other material. NMV P139341–P139342, P139344, P139347–P139349, P139967, P139974, P147051–P147054, from the same locality as the holotype.

Horizon. Wenlock Series, Bylands Siltstone.

Diagnosis. Glabella narrowest at lunette. Facial suture with distinct flexure opposite (tr.) lunette, diverging gently forwards behind flexure, converging forwards in front of flexure. Librigena much wider (tr.) than fixigena posteriorly; posterior margin of librigena markedly concave in outline; genal spine long. Pygidium gently convex; holcos continuous but very shallow posteriorly.

Remarks. The rostral plate and hypostome of *Thomastus aops* sp. nov. are unknown. The pygidium on one of the specimens appears to have a weakly defined axis (Pl. 2, fig. 10), which occupies about half the sagittal length of the pygidium, is about as wide anteriorly as long, and narrows strongly backwards to a well-rounded terminus. Another specimen has four pairs of muscle scars arranged in backwardly converging rows on the anteromedial part of the pygidium (Pl. 2, fig. 7); the scars are more distinct on the internal mould than on the exterior of the exoskeleton, are circular, and successively decrease in size posteriorly. The cephalon of the same specimen appears also to have three or four pairs of very poorly defined muscle scars on the internal mould of the glabella.

Thomastus aops is most easily distinguished from *T. thomastus* by its longer genal spine and more deeply embayed posterior librigenal margin (Table 1). Additional points of difference in *T. aops* are that the facial suture is not evenly curved but has a distinct flexure opposite the lunette, just behind the midlength of the cephalon in dorsal and lateral profiles (Pl. 2, figs 1–2); the facial suture is not exsagittally aligned at its posterior end but diverges forwards as far as the flexure; the lateral pygidial margin is not arched upwards; and the pygidial doublure is evenly curved rather than angular in cross section anteriorly. Small pygidia (14–20 mm wide) of *T. aops* are relatively wider than those of *T. thomastus* of similar size, whereas larger pygidia of *T. aops* have L:W ratios falling in the lower part of the range of *T. thomastus* (Text-fig. 3). Some other apparent differences, such as the slightly deeper cephalic axial furrows, the lower convexity of the cephalon and pygidium, and the continuation of the holcos posteromedially, are difficult to assess given the greater tectonic flattening suffered by specimens of *T. aops* in comparison with specimens of *T. thomastus* preserved in concretions.

Thomastus jutsoni (Chapman, 1912)

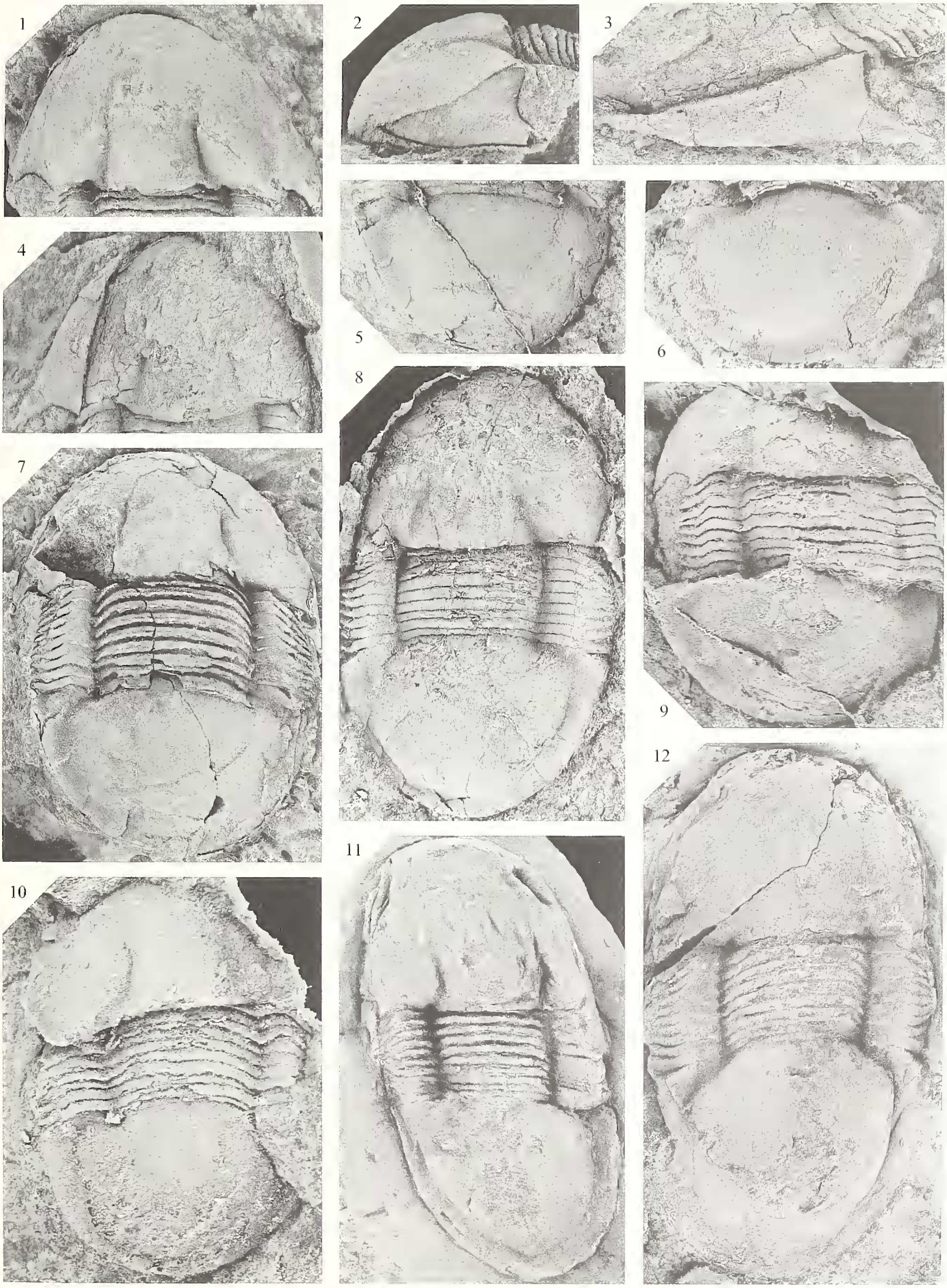
Plate 2, figures 11–12

1912 *Illaenus jutsoni* Chapman, p. 295, pl. 61, figs 4–5.
1952 *Illaenus jutsoni*; Gill, p. 42.
1952 *Illaenus* aff. *jutsoni* Chapman; Gill, p. 43, pl. 1, fig. 1.
1953 *Thomastus jutsoni*; Öpik, p. 22.
1953 *Illaenus jutsoni* Chapman 1912; Öpik, p. 25, pl. 9, fig. 80.
?1955 *Thomastus* sp. indet.; Whiting, p. 32.
1965 *Thomastus jutsoni* (Chapman); Gill, p. 24, pl. 6, fig. 1.
1971 *Illaenus jutsoni* Chapman; Kobayashi and Hamada, p. 127.

EXPLANATION OF PLATE 2

Figs 1–10. *Thomastus aops* sp. nov.; locality PL206, Bylands Siltstone (Wenlock), Bylands, Victoria. 1–2, 9, NMV P139345; dorsal exoskeleton. 1, internal mould, dorsal view of cephalon. 2, internal mould, lateral view of cephalon. 9, latex cast, dorsal view. All ×2·5. 3–4, NMV P139968; latex cast of dorsal exoskeleton. 3, dorsolateral view of cheek; ×3·75. 4, dorsal view of cephalon; ×2·5. 5, 7, NMV P139339; dorsal exoskeleton. 5, latex cast of pygidium, dorsal view; ×1·5. 7, internal mould of dorsal exoskeleton, dorsal view; ×1·6. 6, NMV P139340; pygidium and incomplete thorax; latex cast of pygidium, dorsal view; ×3. 8, NMV P139969, holotype; dorsal exoskeleton; latex cast, dorsal view; ×2. 10, NMV P139346; dorsal exoskeleton; latex cast, dorsal view; ×3.

Figs 11–12. *Thomastus jutsoni* (Chapman, 1912); Anderson Creek Formation (Wenlock), Melbourne district, Victoria. 11, NMV P12299, holotype; locality PL1372; internal mould of dorsal exoskeleton, dorsal view; ×2. 12, NMV P14719; locality PL1373; internal mould of dorsal exoskeleton, dorsal view; ×1·5.



SANDFORD and HOLLOWAY, *Thomastus*

1971 *Thomastus jutsoni*; VandenBerg, p. 3.
1974 *Thomastus* (?) *jutsoni*; Kobayashi and Hamada, p. 30.
1974 *Bumastus* (?) *jutsoni*; Kobayashi and Hamada, p. 33.

Holotype. Internal mould of dorsal exoskeleton NMV P12299, figured Chapman (1912, pl. 61, figs 4–5), Öpik (1953, pl. 9, fig. 80), Gill (1965, pl. 6, fig. 1), Plate 2, figure 11; from locality PL1372, a former quarry site in Bulleen Road, Bulleen, 12 km east-north-east of Melbourne city centre, Victoria.

Other material. Internal mould of dorsal exoskeleton NMV P14719, from locality PL1373, a sewerage excavation in Hill Road, North Balwyn, Melbourne district, Victoria.

Horizon. Wenlock Series; Anderson Creek Formation.

Diagnosis. Occipital furrow very weakly defined. Glabella narrowing forwards as far as occipital furrow, subparallel just in front of occipital furrow, subsequently expanding gently forwards to lunette; width at lunette slightly less than width at posterior cephalic margin. Pygidium rather elongate, 80–90 per cent. as long as wide; doublure very wide, *c*. 30 per cent. sagittal length of pygidium.

Remarks. Both specimens are poorly preserved. As noted by Öpik (1953, p. 25), the description of the holotype by Chapman (1912) is very inaccurate, particularly in the account of eyes, which apparently do not exist, and the form of the facial suture and genal spine, which are not preserved. Crushing of the specimen appears to have caused the sagittal ridge on the cephalon described by Chapman, and has probably also exaggerated the depth of the holcos. The specimen from North Balwyn retains the right librigena, which has been flexed downwards so that it stands vertically, the resulting fracturing of the cephalon obscuring the facial suture; the librigena is very poorly

TABLE 1. Comparison of diagnostic characters of *Thomastus thomastus*, *T. aops* and *T. jutsoni*.

	T. thomastus	*T. aops*	*T. jutsoni*
Narrowest part of glabella	At lunette	At lunette	Posterior to lunette
Occipital furrow	Absent	Absent	Weak
Facial suture	Evenly curved, converging forwards	Distinct flexure opposite lunette, diverging forwards behind flexure, converging forwards in front of flexure	Unknown
Posterior width of librigena	Slightly greater than width of fixigena	Much greater than width of fixigena	Much greater than width of fixigena?
Posterior margin of librigena	Gently concave	Strongly concave	Unknown
Genal angle	Orthogonal or with very short spine	Long genal spine	Short spine?
Holcos	Non-existent posteriorly	Continuous but shallow posteriorly	Unknown
Lateral margin of pygidium	Gently arched	Not arched	Not arched
Pygidial doublure	Narrow, angular in cross section anteriorly	Narrow, evenly curved in cross section anteriorly	Very wide